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Animal behaviour

An infanticide attempt by a free-roaming feral stallion (*Equus caballus*)

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Infanticide by adult males occurs in a variety of species. While infanticidal attacks have been documented in several equid species in captivity, it has never been witnessed in free-roaming feral horses. I report an infanticide attempt by a free-living feral stallion on a recently born female foal. The stallion picked up the foal by the shoulders, tossed it around twice and bit in on the neck several times. The dam of the foal charged the stallion and successfully protected her foal from additional attacks. The foal survived the attack and later weaned successfully. The stallion recently took over the band and was excluded as the sire through genetic analysis. While this type of attack is rare, this case lends support to the sexual selection hypothesis and further demonstrates that equids have evolved with the risk of infanticide. Furthermore, it shows that maternal protectiveness can be successful against attacks by infanticidal males.

Keywords: feral horse; maternal protectiveness; sexual selection hypothesis

1. INTRODUCTION

Infanticide, while rare, is a widely documented phenomenon in several mammal species including primates (Hrdy 1977; Crockett & Janson 2000; Watts et al. 2002), carnivores (Packer & Pusey 1983; Swenson et al. 1997) and rodents (Coulon et al. 1995; Vom Saal et al. 1995; Blumstein 2000). Male infanticide is generally considered to be an adaptive strategy whereby the interbirth interval is reduced, and the male can sire the subsequent offspring (Van Schaik 2000). Sexual selection infers a benefit to the reproduction of infanticidal males provided that only unrelated infants are killed, since infanticide is costly to males if related offspring are killed (Van Schaik 2000). Thus, recognition of paternity plays a key role in the evolution of this strategy.

With the exception of red deer (Cervus elaphus; Bartos & Madlefousek 1994) and the hippopotamus (Hippopotamus amphibius; Lewison 1998), the majority of cases of infanticide involving ungulates are reported in equids, including the horse (Equus caballus; Duncan 1982), Przewalski horse (Equus przewalskii; Ryder & Massena 1988; Feh & Munkhtuya 2008), mountain zebra (Equus zebra; Penzhorn 1984) and Burchelli's zebra (Equus burchelli; Pluhacek & Bartos 2000). Feral horses are unusual among ungulates in that they form stable harem-type groups

year-round, consisting of one or more mares and usually one but sometimes several stallions (Linklater 2000). Band stallions are known to obtain high paternity within their band (Bowling & Touchberry 1990), but sneak copulations occur and mares change bands, which can result in paternity differences between foals (Miller 1981). In feral horses, infanticide has never been documented in the wild, but feticide may occur (Berger 1983). Feral mares have been shown to increase maternal protectiveness in response to paternity uncertainty (Cameron *et al.* 2003), which suggests that females have evolved to protect their foals from attacks against males. Here, I document a case of a resident band stallion attacking a young foal shortly after birth in a free-roaming situation.

2. MATERIAL AND METHODS

A feral horse population in the Virginia Mountain Range outside Reno, Nevada, was observed intensively from 2004 to 2008 for the purposes of another study. The total population fluctuated from over 1200 horses down to 1000 horses over the course of those years. The Nevada Department of Agriculture is responsible for managing the horses and the population size was and is still controlled by removals and contraception. The study included approximately 300 known individuals. Horses were habituated to human observers. The band in which the attack occurred was seen on a weekly basis to determine band membership and fidelity. At the time of the attack, the band consisted of two adult stallions, two adult mares, one juvenile male and one male foal. The band was being observed due to a recent birth of a foal and from that time, ad libitum observations were recorded until the end of the incident. All aggressive behaviours were documented and a description of these behaviours can be found in an equid ethogram (McDonnell & Haviland 1995). Genetic data were taken from faecal samples from the foal, dam and band stallion. Paternity was assessed using 12 polymorphic horse-specific microsatellites.

3. RESULTS

During routine behavioural observations on 12 April 2005, an infanticide attempt was witnessed. The band was passed at 15.40, while observing another band. At that time, the foal was not born. At 16.14, while passing the band again, the mare had recently given birth. A new female foal was covered with mucous and lying on the ground next to her dam. The foal was estimated to be no more than 1 hour old when the attack occurred and had not attempted to stand up. The rest of the band, including the dominant band stallion (stallion A), were all resting near the mare and newborn foal. At 16.20, a stallion (stallion B) from a nearby band called out and approached the mare. She immediately gave a head threat towards stallion B. The foal attempted unsuccessfully to stand up. The band stallion (stallion A) lunged towards the mare and foal and immediately bit the foal on the neck several times. Stallion A subsequently picked the foal up by the shoulders twice and shook it around several times. The foal was dropped to the ground and subsequently bitten and kicked by the front legs of stallion A several times. The attack lasted approximately 1 min. During the attack, the mare defended her foal by charging, biting and kicking stallion A, which led to the end of the attack. After the attack, stallion A had several aggressive interactions with stallion B and continued to try to herd the mare away from the area. The mare continued to charge and head threat stallion A when he came near her and she remained in her position over the foal. Stallion B called out again, which led to another aggressive interaction between stallion A and the mare. While the foal appeared to be in shock, there was no visible major damage, but she suffered minor superficial wounds. The foal stood up at 17.39 and nursed at 17.47, and at that time the observations ended. The band was observed over the course of the next year and the foal successfully weaned.

The attacker (stallion A) was excluded as the father of the foal through microsatellite DNA analysis.

4. DISCUSSION

The attack was unmistakably an infanticide attempt as it was similar to other reported attacks in equids (Duncan 1982; Feh & Munkhtuya 2008). Most infanticidal attacks by stallions occur before the foal reaches one month (Pluhacek & Bartos 2000) and in this case, the foal was recently born. Infanticide imposes direct fitness consequences on the parents of the offspring, especially the mother. Such costs include decreased inclusive fitness, energy expenditure and the loss of investment (Ebensperger 1998). Females should adopt counterstrategies against infanticide in order to maximize their lifetime fitness (Ebensperger 1998). These counterstrategies include fighting back, having close associations with males for infant protection, prolonged receptivity, territoriality, avoidance and termination of infant care (Ebensperger 1998). In horses, mares will defend against infanticidal attacks (Feist & McCullough 1975; Ryder & Massena 1988) by generally positioning themselves between their foal and another approaching horse, even if no direct threat is apparent (Crowell-Davis & Houpt 1986). This protective behaviour was witnessed during the attack, as the mare defended her foal by charging and biting the stallion. She also tried to position herself between the stallion and foal and stood over the foal after the incident. All of these actions appeared to stop the attack and prevent further assaults.

There were several factors that possibly led up to this attack. First, genetic analysis confirmed that the band stallion was not the sire. Second, the band stallion had recently taken over the band and shared the band with another adult stallion. Owing to these factors, there was a high level of paternity uncertainty that may have influenced the decision to attack. Little is known about how males detect paternity, but evidence in primates suggests that males detect paternity by consort time, phenotypic matching or the amount of time spent within the troop during the mating season (Buchan et al. 2003). In this case, the male did not have a consortship with the female, nor did he spend anytime with this female during the previous mating season. The uncertainty of paternity has been postulated as proximate cause of an infanticide attempt (Borries et al. 1999) and is believed to be the major cause in this particular case.

Recently, infanticide in equids was suggested to be in response to human intervention (human disturbance hypothesis), as most cases have been associated with unnatural environments and introductions of foreign males (Feh & Munkhtuya 2008).

While humans may influence infanticide attacks, most documented cases have also been associated with foreign males. For example, in equids, attacks end after males and females have been housed together for longer periods of time (Ryder & Massena 1988), suggesting that the unnatural conditions do not explain infanticide. In addition, many infanticidal events in the wild are associated with contact with foreign males, and attacks are generally attributed to these males. In this case, the male was relatively foreign in the band and several factors increased the level of uncertainty of paternity (i.e. multi-stallion band, recent takeover, no consortship before the foal was born). In addition, the similarity of attacks between equid species, maternal protectiveness and genetic data all suggest that equids have evolved with and respond to infanticide risk. Furthermore, infanticide has been postulated as a main explanation for primate social structure and the evolution of yearround male-female associations (Kappeler 1997; Van Schaik & Kappeler 1997). Feral horses have similar social structure to primates and male harassment plays a primary role in social structure (Linklater et al. 1999).

This was the only attack witnessed during 3 years of behavioural observations. Several studies suggest that feticide may be more adaptive in horses (Berger 1983), and there are some suggestions that infanticide is low risk in equids (Feh & Munkhtuya 2008). However, several foals go missing and are found dead every year in all populations, even when no predators are present. While these deaths could be due to numerous factors, infanticide is a possible cause of some deaths. Furthermore, foals not sired by the band stallion have lower survival rates to weaning (M. E. Gray 2008, unpublished data). All of this makes a witnessed event and possible causes important to document. To my knowledge, this is the first documentation of this type of attack in feral horses in a free-living situation and lends support to the role of infanticide in social structure.

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